Recovery following experimental harvesting of *Laminaria longicruris* and *Laminaria digitata* in southwestern Nova Scoti

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*Laminaria* population variables and understory community composition were monitored just prior to, and for two summers following, a September 1980 experimental total harvest of *L. longicruris* De la Pylaie and *L. digitata* (L.) Lamouroux within two plots in Lobster Bay, Nova Scotia. Both plots, distinguished mainly by depth, were characterized by high *Laminaria* standing crop biomass and no recent history of extensive sea urchin grazing. Within the shallower (2-3 m below MSL) plot recovery could not be assessed due to plant life expectancies less than one year and large natural variations in the population characteristics of both species. Within the deeper (3-4 m below MSL) plot *L. longicruris* regrew cropped biomass and attained maximum observed abundance within one year. Both *Laminaria* species required two years to mature to pre-harvest population characteristics. Survivorship of 0-1 year old and mature populations of both species was

generally low (0-67% per year); however, the higher maximum life expectancy of *L. digitata* (>4 years vs. 2 years) can result in that species persisting to the disadvantage of *L. longicruris*. The maximum yield per recruit for both species occurred the summer after harvesting. Analysis of understory community composition for both harvested plots and their adjacent controls distinguished the harvested plots one summer after harvesting from all others. In the shallow site the distinction could be unequivocally attributed to a significant increase in the standing crop biomass of some epiphytic and/or annual species, but it is doubtful the distinction is attributable to harvesting. In the deeper site the distinction was less clear, and in neither site was there evidence of a critical change in the understory community. Management implications for the commercial harvest of *Laminaria* are discussed. A yearly harvest during late spring or early summer is recommended for maximizing yield.

Key words: harvest, *Laminaria*, marine algae, resource management, seaweed

# TABLE OF CONTENTS

ABSTRACT..... i
TABLE OF CONTENTS..... iii
LIST OF TABLES..... iv
LIST OF FIGURES..... v
ACKNOWLEDGEMENTS..... vi
INTRODUCTION..... 1
SITE DESCRIPTION..... 3
METHODS..... 6
RESULTS..... 9
Understory community..... 9
*Laminaria* recovery..... 15
*Laminaria* growth and survivorship..... 20
DISCUSSION..... 30
LITERATURE CITED..... 36

## LIST OF TABLES

Table 1: Taxa recorded in the quantitative quadrat collections within the control and harvest plots of sites S and D in the summer of 1980 and 1981. .....12

Table 2: Ecological parameters for the control (C) and harvest (H) plots of sites S and D in 1980 and 1981. .....14

Table 3: Population characteristics of *Laminaria longicruris* and *Laminaria digitata* within the harvest (H) and control (C) plots of sites S and D during the summers of 1980-82. .....16

Table 4: Survivorship of unperturbated and recovering populations of *Laminaria longicruris* and *Laminaria digitata* for different depths at site D. .....23

## LIST OF FIGURES

Figure 1: Standing crop biomass of L. longicruris and L. digitata at sites S and D within Lobster Bay, southwest Nova Scotia. .....4

Figure 2: Diagrammatic representation of sites S and D within Lobster Bay, Nova Scotia; and the locations of the biomass assessment transects, tagged L. longicruris and L. digitata quadrats, and the harvest plot outline. .....5

Figure 3: Cluster diagram of 'plot-year' similarity for the understory communities of sites S and D. (C = control plot, H = harvest plot) .....10

Figure 4: Total plant length (cm) histograms for L. longicruris within the harvest and control plots at sites S and D during the years they were assessed. (1980 = pre-harvest; 1981+ = post-harvest) .....17

Figure 5: Total plant length (cm) histograms for L. digitata within the harvest and centrol plots at sites S and D during the years they were assessed. (1980 = pre-harvest; 1981+ = post-harvest) .....18

Figure 6: Percentage survivorship of unperturbated and recovering (0-1 year old, harvested September 1980) populations of L. longicruris and L. digitata at different depths within site D. .....22

Figure 7: Mean stipe length (SL), lamina length (LL) and total length (TL) of unperturbated and recovering (0-1 year old, harvested Sept 1980) populations of L. longicruris and L. digitata within site D. (Minimum n=13) .....25

Figure 8: Seasonal growth and attrition of L. longicruris and L. digitata lamina within site D for the period March 1982 until April 1983. (Minimum n=11) .....27

Figure 9: Cohort biomass of 0-1 year old L. longicruris and L. digitata recovering from a September 1980 harvest within site D and first monitored in May 1981. .....28

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## INTRODUCTION

The desire to understand the characteristics and role of the seaweed community in nearshore ecosystems and their implications for eastern Canadian fisheries management has produced several contributions during the past few years (see Pringle *et al*. 1980, Wharton and Mann 1981). However, nearly all address the role of this community in relation to higher trophic levels, in particular the lobster, and the possible detrimental consequences of lost seaweed production. We still have little information on, and lack an understanding of, the population and community characteristics of seaweeds, the notable exception being *Chondrus crispus* Stackhouse. This species is presently the most economically important seaweed in the region, and has been the subject of intensive resource management research since 1975 (Pringle and Sharp 1980). More recently attention has started to focus on the kelp species (Laminariales). Kelp is harvested in various parts of the world for dried foodstuffs and for alginate (Pringle and Sharp 1980). In southwestern Nova Scotia, Canada, *Laminaria* was harvested from 1940-1949 and periodically since then. The quantities were relatively small (<3000 MT, wet) and apparently sustainable but there were reports of harvested populations not recovering (Sharp 1980).

To improve our understanding of the dynamics and characteristics of *Laminaria* populations in Nova Scotia, as recommended by Pringle *et al*. (1980), this study presents the results of a three year program to assess the impact of a total *Laminaria* harvest at two sites within a *Laminaria* dominated seaweed community in Lobster Bay in the southwestern part of the province. This area was chosen because of no recent history of extensive sea urchin grazing, which has detrimentally affected most kelp beds in Nova Scotia (Chapman, 1981), and it is the area where harvesting is likely to occur. Recent discussions with executives of the marine plant industry in Nova Scotia indicate renewed interest in *Laminaria*. If their corporate plans are realized, they anticipate a demand for large quantities of the resource in the foreseeable future.

## SITE DESCRIPTION

To overcome discontinuities in hard substrate with depth, two study sites located within 5 km of each other in Lobster Bay, Nova Scotia ($43^{o}41'N \times 65^{o}52'W$), were chosen for high Laminaria biomass and accessibility. The shallower site (S) is east-facing from a low reef exposed only at low tide and the deeper site (D) faces west off a small island in the bay. The sites are similar in exposure to wave actien and are characterized by temperatures and salinities ranging from -1 to $17^{o}C$ and 28 to 33 $^{o}/oo$, respectively. Intertidal and shallow subtidal areas occasionally experience lower salinities with an ebb tide during spring melt and suffer from ice scouring during severe winters.

The substrate for plants at both sites varies with depth from smaller to larger rocks. Mean substrate attenuations for the two sites are 12.4±6.3 cm (n=320) and 25.5±13.9 cm (n=1200) for sites S and D, respectively. Natural Laminaria standing crop biomass distribution with depth is presented in Figure 1.

Figure 1: Standing crop biomass of L. longicruris and L. digitata at sites S and D within Lobster Bay, southwest Nova Scotia.

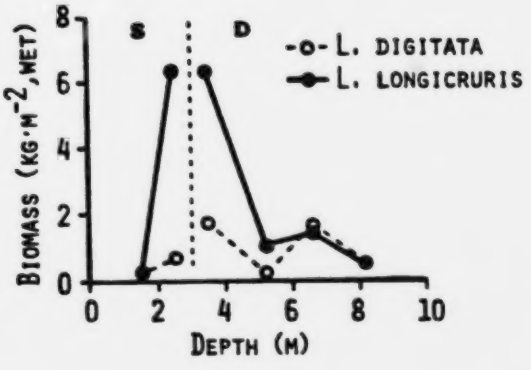
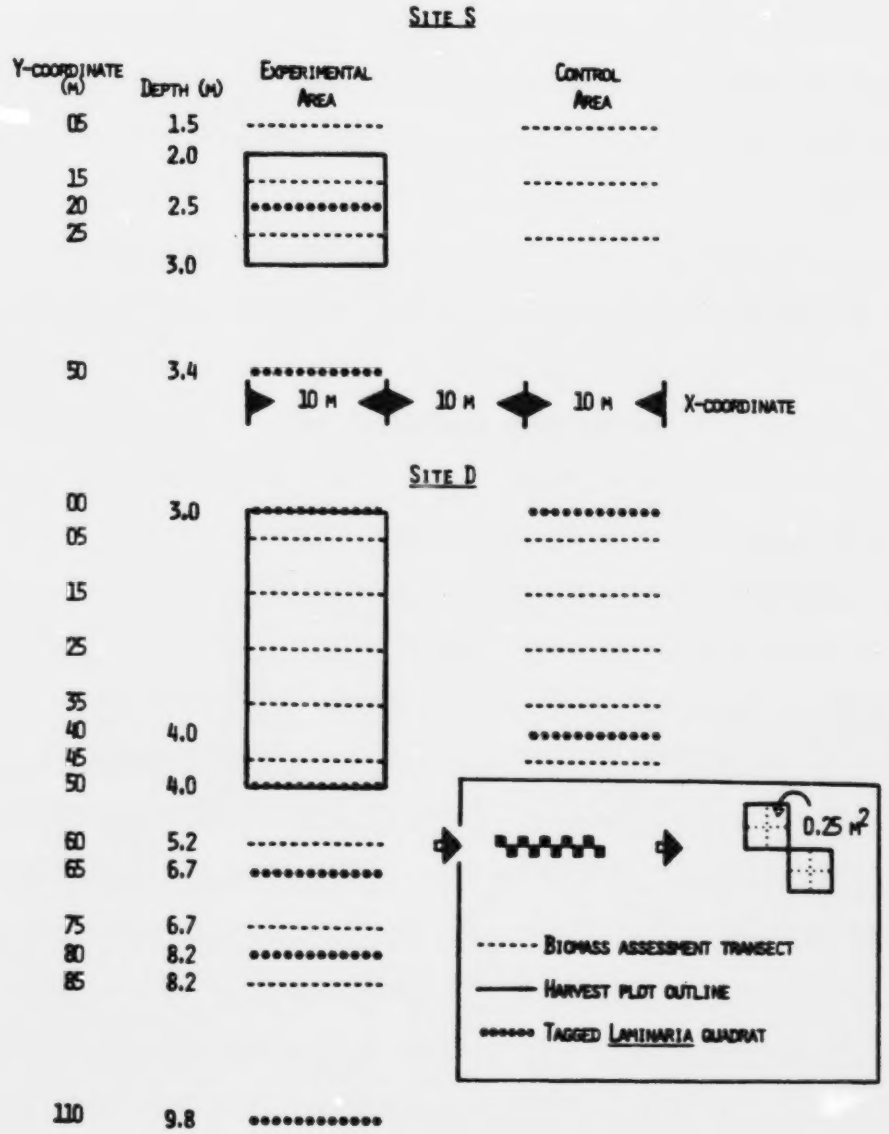


Figure 2: Diagrammatic representation of sites S and D within Lobster Bay, Nova Scotia; and the locations of the biomass assessment transects, tagged L. longicruris and L. digitata quadrats, and the harvest plot outline.



## METHODS

Figure 2 portrays the layout and sampling format of sites S and D. Precise location of the experimental plots and permanent quadrats for monitoring tagged plants was facilitated by placing flagged aluminum eye-bolts in the substrate. All field maintenance, collections and measuring required the use of SCUBA.

Harvest and control plot biomass assessments at sites S and D were obtained for all species in the summers of 1980 and 1981, and for Laminaria at site D also the summer of 1982. All Laminaria plants greater than 50 cm total length were enumerated within each of the forty 0.25 $m^2$ quadrats comprising each assessment transect. Following Laminaria enumeration the most representative 0.25 $m^2$ quadrat of each 1.0 $m^2$ quadrat was collected using an underwater airlift fitted with a 3 mm mesh collecting bag. The choice of collected quadrats was biased when necessary toward obtaining sufficient data on Laminaria population statistics. All plant material within each collected quadrat was sorted to species, and weighed both wet and, with the exception of Laminaria 10 cm dry, (24 hr. at 100C). For site D collections, the biomass of Phyllophora brodiaei (Turner) J. Agardh, P. membranifolia (Goodenough and Woodward) J. Agardh, and Chondrus crispus Stackhouse was corrected for bryozoan encrustation. C. crispus was further separated into fronds greater or less than 10 cm. Individual plants

of L. longicruris and L. digitata >10 cm total length were counted and the following variables measured: stipe length, lamina length, stipe weight, lamina weight, number of lamina, maximum lamina width, reproductive? (Yes or No), distance to sorus, sorus weight. Environmental conditions and substrate characteristics for both sites were also recorded. In early September 1980, immediately following the control and harvest plot assessments for both sites, all Laminaria plants within and overlapping the harvest plots were detached at or near the holdfast by SCUBA divers using long sharp kitchen knives.

Laminaria growth and mortality data were obtained by regularly counting and measuring tagged plants of each species within two site S and seven site D quadrats (1 m x 10 m). All plants greater than 50 cm total length within one site S and two site D harvest plot quadrats were tagged with individually numbered cable ties and first measured the summer following harvesting (1981). The same procedure, but at different starting dates, was followed for the six quadrats not in the harvest plots. The plant measurements are those listed earlier for the assessment transects with the exception of weight determinations. Beginning in March 1982, holes (5 mm diameter) were punched 5 cm above the meristem of each remaining plant and some newly tagged plants to measure linear lamina growth and attrition

(Mann 1973). The tagged plant quadrats were monitored until April 1983.

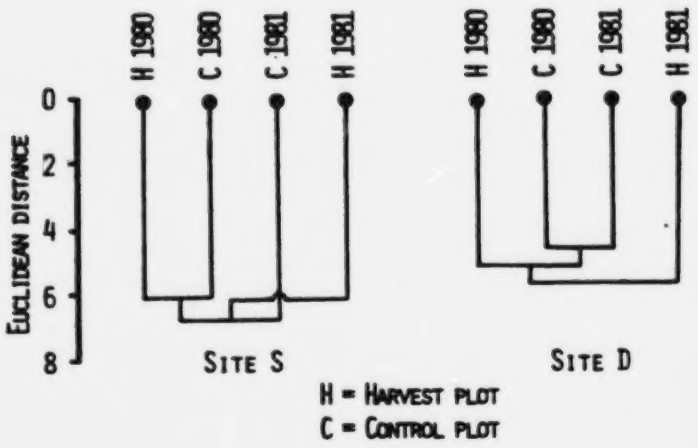
Each day's records were transcribed from underwater slates to computer coding forms as soon as possible by the person who collected the information. The data were edited and analysed by the Control Data CYBER 170-730 computer operated by Dalhousie University, Halifax. All numerical analyses used the BMDP-77 packages prepared by the Health Sciences Computing Facility, Department of Biomathematics, School of Medicine, University of California, Los Angeles.

## RESULTS

### Understory community:

Understory community characteristics were measured and monitored until the *Laminaria* population recovered substantially from harvesting, which was interpreted to be the summer following harvesting (1981). A cluster analysis of all 80 site S and all 200 site D quadrats, without distinction of harvest and control plots or year, in separate analyses produced no recognizable groups. This was not unexpected because of the *a priori* requirement that the harvest and control plots be similar and within-plot variability contributed by the patchiness of the more abundant species. This latter consideration was emphasized by the rocky substrate. Considering the plots as entities, Figure 3 distinguishes the harvest plot in 1981, the summer following harvesting, from all others at both sites using standardized Euclidean distance as a measure of 'plot-year' community similarity. Linkage order is the result of a centroid clustering procedure. Standardized Euclidean distance is an appropriate similarity measure because of its equal sensitivity to all species. It is effective in distinguishing plot-year entities by comparing cumulative variation in species biomass between pairs of entities, but because of its statistical nature is inadequate for interpreting the distinctions from an ecological viewpoint.

Figure 3: Cluster diagram of 'plot-year' similarity for the understory communities of sites S and D. (C = control plot, H = harvest plot)



A more rigorous scrutiny of the difference between the 1981 harvest plots and the other plots is presented in Table 1. When analyzed individually, the species which contributed the most to the distinction of H1981 from the other plots at site D, specifically Chordaria flagelliformis (Müller) C. Agardh and Polysiphonia sp., did not have significantly different distributions for the control versus harvest plots in either 1980 or 1981. This weakens the validity of the distinction in Figure 3 and alludes to the possibility of misinterpreting results of clustering analyses. Overall, the trend for site D is a significant decrease in the abundance of several species relative to the preharvest state; however, increase in the abundance of two species was recognized. The epiphyte Cystoclonium purpureum (Hudson) Batters displayed the strongest response, with H1981 biomass increasing 170% over H1980 biomass ($p=.02$) compared with only a 65% increase for C1981 relative to C1980 ($p=.32$). Three other species, Cladophora sp. (-), Corallina officinalis L. (+) and Membranoptera alata (Hudson) Stackhouse (-) are also interpreted as the most apparent indicators of change in the understory community because of their high abundance and contribution to Euclidean distance. Ceramium rubrum (Hudson) C. Agardh, Euthora cristata (L. ex Turner) J. Agardh and Palmaria palmata (L.) Greville were not included in the cluster analysis presented for site D since they

Table 1: Taxa recorded in the quantitative quadrat collections within the control and harvest plots of sites S and D in the summer of 1980 and 1981. The variables tabled are those used in judging understory community changes following a 1980 *Laminaria* harvest at each site.

| Species | Site S | | | | | Site D | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | %[a] | Rank[b] | C vs H[c] 1980 | C vs H 1981 | Δ[d] | % | Rank | C vs H 1980 | C vs H 1981 | Δ |
| **CHLOROPHYTA** | | | | | | | | | | |
| *Chaetomorpha atrovirens* Taylor | 0.02 | 25 | ns | ns | | 0.02 | 11 | ns | ns | |
| *Cladophora* sp. | 0.01 | 13 | ns | ns | | 0.56 | 5 | <.05 | ns | - |
| **PHAEOPHYTA** | | | | | | | | | | |
| *Asperococcus echinatus* (Mertens) Greville | <0.01 | 24 | ns | ns | | 0.0 | * | * | * | |
| *Chordaria flagelliformis* (Müller) C. Agardh | 0.12 | 14 | ns | ns | | <0.01 | 1 | ns | ns | |
| *Desmarestia aculeata* (L.) Lamouroux | 0.17 | 18 | ns | ns | | 0.44 | 12 | ns | <.05 | - |
| *Desmarestia viridis* (Müller) Lamouroux | <0.01 | 22 | ns | ns | | 0.02 | 15 | ns | <.01 | - |
| *Fucus vesiculosus* L. | 1.06 | 15 | <.05 | ns | + | 0.0 | * | * | * | |
| *Leathesia difformis* (L.) Areschoug | <0.01 | 16 | ns | ns | | 0.0 | * | * | * | |
| *Saccorhiza dermatodea* (De la Pylaie) Farlow | <0.01 | 3 | ns | ns | | 0.0 | * | * | * | |
| *Scytosiphon lomentaria* (Lyngbye) C. Agardh | 0.01 | 23 | ns | ns | | 0.28 | 18 | <.05 | ns | - |
| **RHODOPHYTA** | | | | | | | | | | |
| *Ahnfeltia plicata* (Hudson) Fries | 0.48 | 26 | <.01 | ns | + | 0.01 | 13 | <.01 | ns | - |
| *Ceramium rubrum* (Huds.on) C. Agardh | 0.04 | 2 | <.001 | ns | + | 1.15 | * | * | * | |
| *Chondrus crispus* Stackhouse (fronds >10 cm) | 34.27 | 6 | ns | ns | | 18.06 | 14 | ns | ns | |
| *Chondrus crispus* (fronds <10 cm) | 56.46 | 10 | ns | ns | | 28.81 | 7 | <.001 | <.001 | |
| *Corallina officinalis* L. | 1.39 | 7 | ns | ns | | 10.18 | 8 | <.05 | ns | +[e] |
| *Cystoclonium purpureum* (Hudson) Batters | 1.05 | 1 | ns | <.01 | + | 0.60 | 3 | <.05 | <.001 | +[e] |
| *Dumontia incrassata* (Müller) Lamouroux | <0.01 | 9 | ns | ns | | 0.0 | * | * | * | |
| *Euthora cristata* (L. ex Turner) J. Agardh | 0.01 | 19 | ns | ns | | 0.14 | * | * | * | |
| *Membranoptera alata* (Hudson) Stackhouse | 0.01 | 17 | <.05 | ns | - | 1.15 | 4 | <.001 | ns | - |
| *Palmaria palmata* (L.) Greville | 2.77 | 8 | ns | <.01 | + | 1.40 | * | * | * | |
| *Phyllophora brodiaei* (Turner) J. Agardh | 1.17 | 12 | ns | <.05 | + | 8.74 | 6 | ns | ns | |
| *Phyllophora membranifolia* (Goodenough and Woodward) J. Agardh | 0.65 | 5 | ns | ns | | 28.16 | 10 | ns | ns | |
| *Polysiphonia* sp. | 0.01 | 19 | <.01 | ns | + | <0.01 | 1 | ns | ns | |
| *Polyides caprinus* (Gunnerus) Papenfuss | 0.29 | 11 | ns | <.01 | - | <0.01 | 17 | ns | ns | |
| *Ptilota serrata* Kützing | <0.01 | 19 | ns | ns | | <0.01 | 9 | ns | ns | |
| *Rhodomela lycopodioides* (L.) C. Agardh | 0.02 | 4 | ns | ns | | 0.30 | 16 | <.05 | ns | - |

[a] Percentage of total site biomass (pre-harvest; excluding *Laminaria*).

[b] Ranked decreasing sum of squares contribution by each species to the Euclidean distance measure separating the 1981 harvest plots from all others as presented in Figure 3. Note that *Ceramium rubrum*, *Euthora cristata* and *Palmaria palmata* were not included in the cluster analysis for site D since they occurred mainly as epiphytes on *Laminaria longicruris*.

[c] Result of a Mann-Whitney U-test for different control (C) plot and harvest (H) plot biomass distributions. For site S: $n_C=n_H=20$; for site D: $n_C=n_H=50$; ns = non-significant result, i.e. $p>.05$

[d] Absolute or relative direction of a detected shift in harvest plot biomass distribution compared to control plot biomass distribution from 1980 to 1981.

[e] H1981 biomass significantly greater ($p<.05$) than H1980 biomass; C1981 biomass not significantly different from C1980 biomass.

occurred mainly as epiphytes on the larger L. longicruris plants and would bias the results of the analysis toward distinction of H1981. Epiphytes were rarely observed on L. longicruris in the H1981 collections.

For site S the distinction of H1981 is less equivocal with the epiphytes C. purpureum and C. rubrum ranking first and second, respectively, in contribution to Euclidean distance. Both species increased considerably in biomass in H1981. C. purpureum was 740% over H1980 biomass and 919% over C1981 biomass, and C. rubrum increased $10^6$% over H1980 biomass and 394% over C1981 biomass. The general trend for those species which demonstrated a significant relative change was an increase in H1981 biomass. Only two relatively unimportant species decreased in abundance. Of those which increased, other than the two species previously mentioned, only P. palmata increased notably, to 771% of H1980 compared with 165% of C1981. It was not necessary to account for epiphytes in the site S analysis since L. longicruris at that site was free of epiphytes.

Table 2 presents some ecological parameters for each plot. For site S, H1981 has the highest mean dry weight ($g \cdot m^{-2}$) and species diversity (H') for the understory community. The increased biomass of C. purpureum and P. palmata is responsible for the high H1981 biomass,

Table 2: Ecological parameters for the control (C) and harvest (H) plots of sites S and D in 1980 and 1981.

| | Site S | | | | Site D | | | |
|---|---|---|---|---|---|---|---|---|
| | H1980 | C1980 | H1981 | C1981 | H1980 | C1980 | H1981 | C1981 |
| Number of quadrats | 20 | 20 | 20 | 20 | 50 | 50 | 50 | 50 |
| Number of species | 17 | 24 | 21 | 22 | 21 | 16 | 17 | 19 |
| Mean dry weight ($g \cdot m^{-2}$)[a] | 266 | 357 | 505 | 457 | 150 | 180 | 181 | 270 |
| Mean number of species (per 0.25 $m^2$ quadrat) | 6-7 | 9 | 9-10 | 9-10 | 10 | 8-9 | 7-8 | 7-8 |
| Species diversity (H')[b] | | | | | | | | |
| (1) All species | 1.10 | 1.47 | 2.08 | 1.80 | 1.51 | 1.33 | 1.20 | 1.93 |
| (2) Excluding *Laminaria* and its epiphytes | 0.74 | 0.66 | 1.55 | 1.14 | 2.03 | 1.78 | 1.92 | 1.72 |

[a] Excluding *Laminaria*

[b] Shannon and Weaver (1949)

and also the high species diversity by diminishing the dominance of C. crispus. For site D no clear distinction of H1981 is evident, the differences in mean dry weight and species diversity being predominantly due to the large between-plot variance in C. crispus biomass.

Laminaria recovery:

By December 1980, three months following the experimental harvest, a visual reconnaissance of the harvest plot at site D confirmed that regrowth of L. longicruris was well in progress. The plants had recovered to a density that made it difficult to distinguish the harvest plot from the surrounding area, and several plants exceeding 3 m in total length were observed. A very small percentage of the plants were reproductive, i.e. the recognition of soral tissue. Site S was not observed because it was not safely accessible at this time of year.

Table 3 summarizes the population characteristics of L. longicruris and L. digitata at sites S nd D during the summers of 1980-82. Figures 4 and 5 present corresponding length histograms describing the population structure of both species. At site S population variables of L. longicruris and L. digitata were still well under pre-harvest values within H1981 and C1981. The length histograms indicate that the populations of both species

Table 3: Population characteristics of Laminaria longicruris and Laminaria digitata within the harvest (H) and control (C) plots of sites S and D during the summers of 1980-82. The data incorporates only those plants greater than 50 cm total length except where otherwise noted.

| | Site S | | | Site D | | | | |
|---|---|---|---|---|---|---|---|---|
| | 1980(H+C) | H1981 | C1981 | 1980(H+C) | H1981 | C1981 | H1982 | C1982 |
| **Laminaria longicruris** | | | | | | | | |
| Mean biomass ($kg \cdot m^{-2}$, wet)[a] | 6.19 | 0.35 | 0.60 | 6.17 | 5.93 | 2.83 | 8.18 | 4.83 |
| Mean plant length (cm) | 288 | 146 | 123 | 270 | 246 | 244 | 332 | 320 |
| Mean plant weight (g) | 373 | 122 | 49 | 406 | 287 | 389 | 692 | 725 |
| Mean density ($n \cdot m^{-2}$) | 16.6 | 2.6 | 10.0 | 15.2 | 20.7 | 7.2 | 11.8 | 6.7 |
| Percentage reproductive | 13.2 | 0.0 | 1.8 | 22.4 | 15.0 | 16.7 | 31.2 | 29.3 |
| **Laminaria digitata** | | | | | | | | |
| Mean biomass ($kg \cdot m^{-2}$, wet)[a] | 0.69 | 0.20 | 0.15 | 1.77 | 0.46 | 2.98 | 1.97 | 3.15 |
| Mean plant length (cm) | 137 | 76 | 87 | 136 | 99 | 139 | 147 | 164 |
| Mean plant weight (g) | 252 | 91 | 110 | 391 | 101 | 372 | 347 | 511 |
| Mean density ($n \cdot m^{-2}$) | 2.7 | 2.1 | 1.3 | 4.5 | 4.4 | 7.8 | 5.7 | 6.2 |
| Percentage reproductive | 28.6 | 17.7 | 44.4 | 29.3 | 8.9 | 35.3 | 28.9 | 44.1 |

[a]Incorporates all plants and is corrected for sampling bias by adjusting plot biomass based on the expected ratio of 4:1 for 'number of plants counted:number of plants collected' within each plot.

Figure 4: Total plant lenght (cm) histograms for L. longicruris within the harvest and control plots at sites S and D during the years they were assessed. (1980 = pre-harvest; 1981+ = post-harvest)

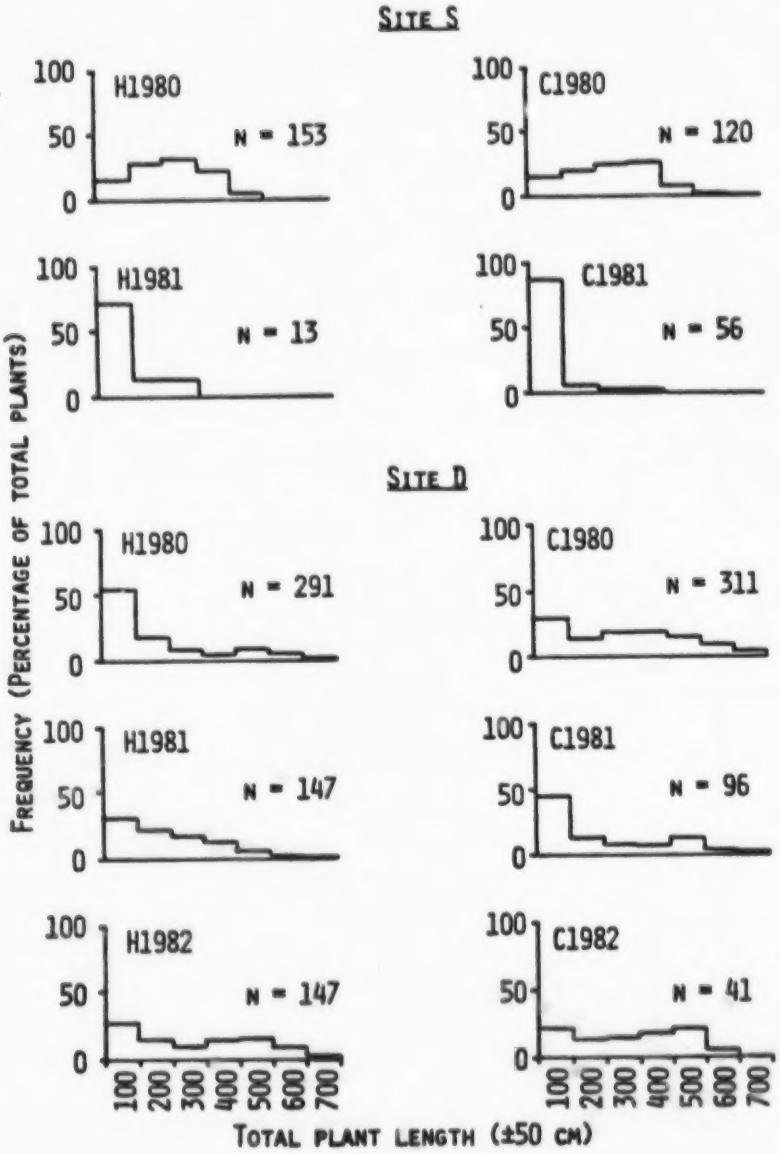
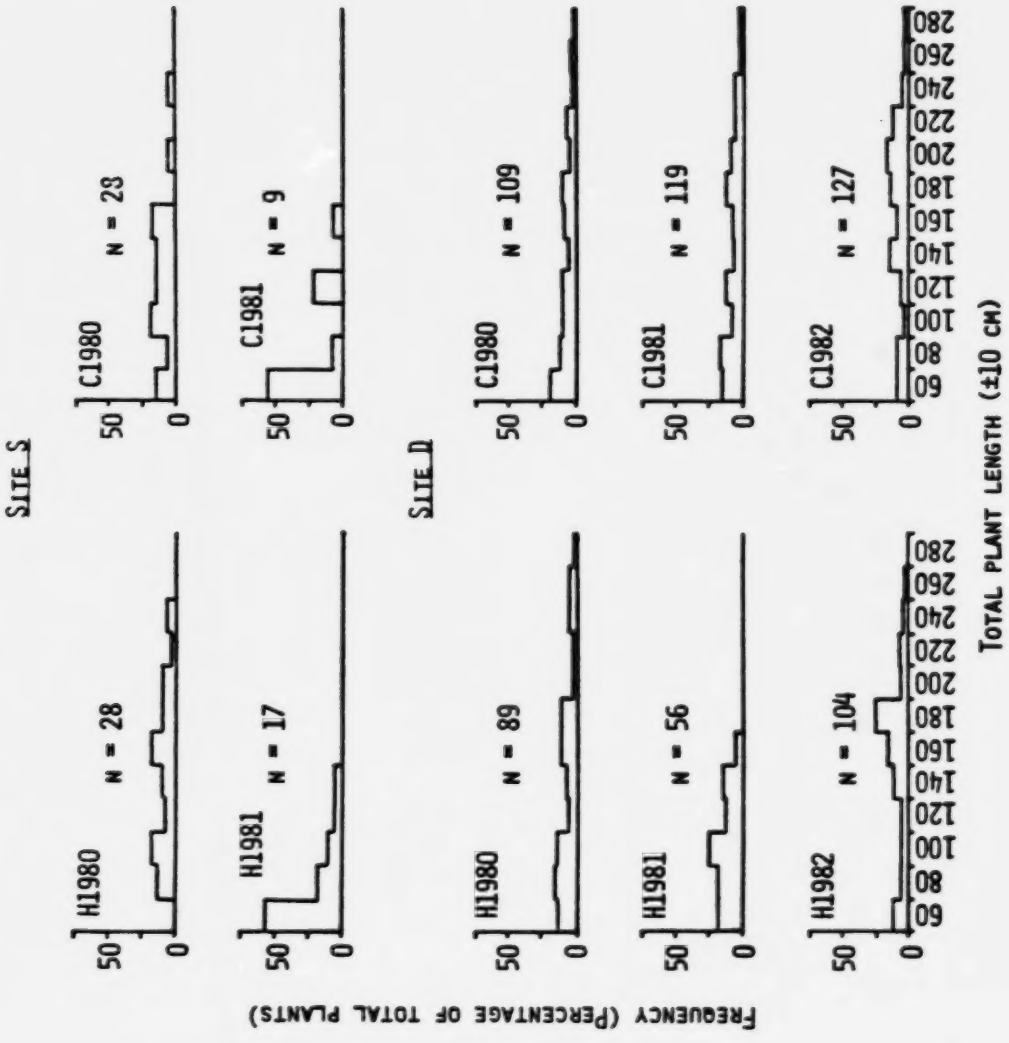


Figure 5: Total plant length (cm) histograms for L. digitata within the harvest and control plots at sites S and D during the years they were assessed. (1980 = pre-harvest; 1981+ = post-harvest)



are shifted toward the smallest length interval, and, by comparison of the control and harvest plot distributions, suggest that both plots are composed mainly of plants less than one year old. There is no evidence that the largest plants in the 1980 plots survived until summer 1981. Site S was not monitored after 1981 because of evidence that the lower biomass of both species in 1981 is due to ice scouring, not the experimental harvest.

Within site D L. longicruris recovered to pre-harvest biomass (96%) the summer following harvesting. Mean plant length and weight were less than pre-harvest values but the corresponding lower biomass was compensated by a 36% increase in plant density. Within H1982 the population variables for L. longicruris exceeded H1980 values. The length distribution for H1982 was substantially similar to that of H1980 with the exception that there were fewer small plants than in H1980. L. digitata required two years (H1982) to recover cropped biomass and attain population characteristics substantially similar to H1980.

Noteworthy in Table 3 is the strong recovery of L. longicruris in H1981 which continues with the highest observed L. longicruris biomass of 8.18 $kg \cdot m^2$ occurring in H1982. This recovery occurs while L. digitata biomass is low relative to the pre-harvest state. Within the

unperturbated (control) Laminaria populations L. longicruris biomass was only 46% and 78% of 1980 biomass in C1981 and C1982, respectively, while L. digitata biomass steadily increased to 178% of 1980 biomass in C1982. The maximum observed ratios of L. longicruris:L. digitata biomass (13:1) and abundance (4.7:1) occurred in H1981. This compares to a pre-harvest ratio of 3.5:1 for both characteristics. A shift toward a more even ratio continued as both the harvest and control plots matured.

For both species two years were required for the percentage of reproductive plants within the population to recover to pre-harvest levels. Only L. digitata had a continually increasing percentage of reproductive plants within the control plot from 1980-82, with the highest observed percentage occurring in 1982.

Laminaria growth and survivorship:

All tagged L. digitata plants (n=43) within one 10 $m^2$ quadrat outside of the harvest plot at site S (depth = 3.4 m below MSL) established August 1980 survived less than one year. Total mortality of L. longicruris was not confirmed until 20 months following tagging, but annual survivorship was estimated to be 14%. For neither species was there evidence of a correlation between mortality risk and plant size. Tagged plants of both species within

the harvest plot quadrat (10 $m^2$) at site S (depth = 2.5 m below MSL) begun the summer following harvesting (May 1981) also had high population moralities. There were fewer plants within the harvest plot and they were monitored less often but 100% mortality of both species was confirmed within 3 months for *L. longicruris* (n=6) and 10 months for *L. digitata* (n=18). Because of the short life expectancies of both species at site S, no useful growth data were acquired.

Survivorship curves for *L. longicruris* and *L. digitata* within the tagged plant quadrats at site D are presented in Figure 6. The data are summarized in Table 4. Variability in mean plant total length between quadrats was noted but there was no consistent evidence of a trend in mortality risk with total length for plants greater than 50 cm in total length. Differences in percentage annual survivorship are thus attributed mainly to depth.

Interpretation of the survival rates indicates longevity of *L. longicruris* and *L. digitata* to be highest at 3-4 m below MSL for both the unperturbated and recovering populations. Within the recovering population no *L. longicruris* and only a few *L. digitata* plants survived two years. By comparison of the survivorship rates within the unperturbated population *L. digitata* is the longer-

Figure 6: Percentage survivorship of unperturbated and recovering (0-1 year old, harvested September 1980) populations of L. longicruris and L. digitata at different depths within site D.

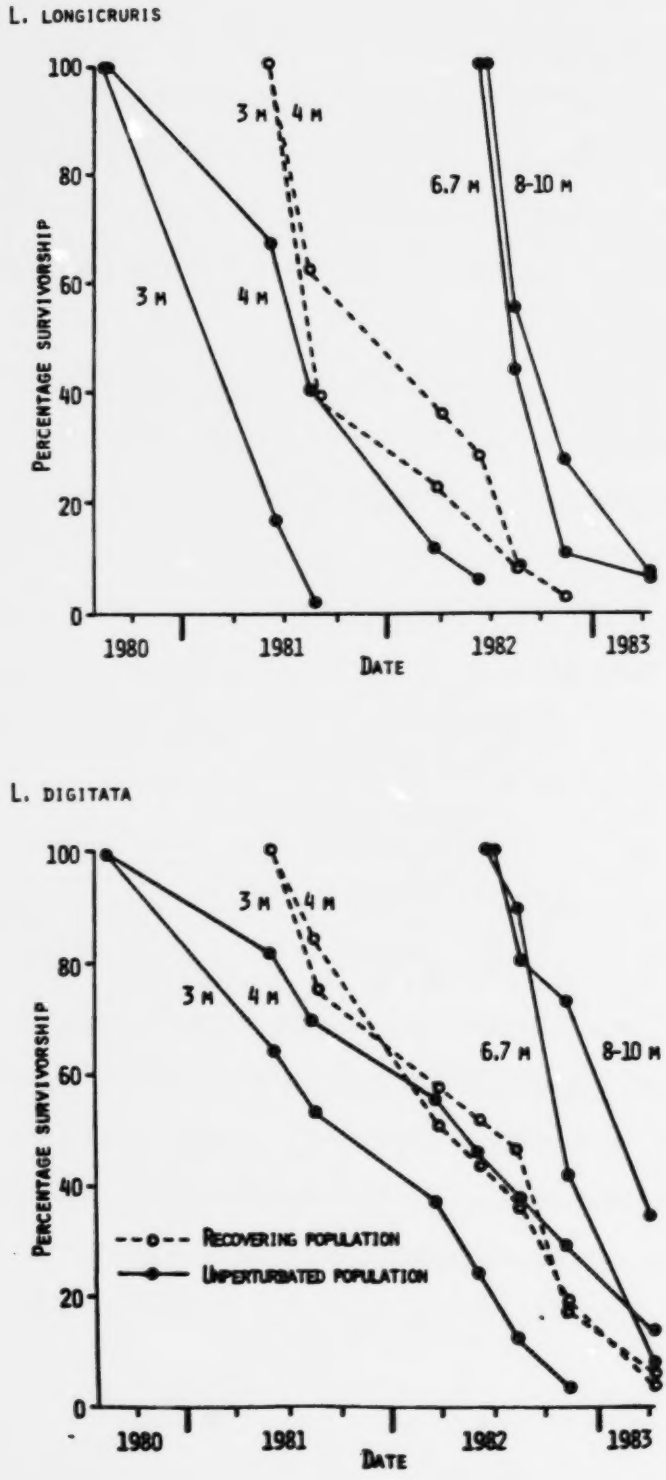


Table 4: Survivorship of unperturbated and recovering populations of Laminaria longicruris and Laminaria digitata for different depths at Site D.

| | Unperturbated population | | | | Recovering population[a] | |
|---|---|---|---|---|---|---|
| Depth (m below MSL) | 3.0 | 4.0 | 6.7 | 8-10 | 3.0 | 4.0 |
| Date monitoring begun | 4 Aug 80 | 12 Aug 80 | 17 Jun 82 | 28 Jun 82 | 27 May 81 | 1 Jun 81 |
| L. longicruris | | | | | | |
| Initial n | 138 | 120 | 46 | 111 | 26 | 71 |
| Initial plant length (cm) | | | | | | |
| (1) Mean | 320 | 230 | 560 | 240 | 210 | 260 |
| (2) 1 S.D. | 160 | 190 | 190 | 190 | 110 | 150 |
| Percentage annual survivorship[b] | 7 | 51 | 0 | 0 | 25 | 33 |
| L. digitata | | | | | | |
| Initial n | 63 | 113 | 26 | 51 | 35 | 53 |
| Initial plant length (cm) | | | | | | |
| (1) Mean | 130 | 100 | 123 | 90 | 110 | 90 |
| (2) 1 S.D. | 60 | 60 | 10 | 50 | 30 | 30 |
| Percentage annual survivorship[b] | 57 | 67 | 0 | 15 | 49 | 48 |

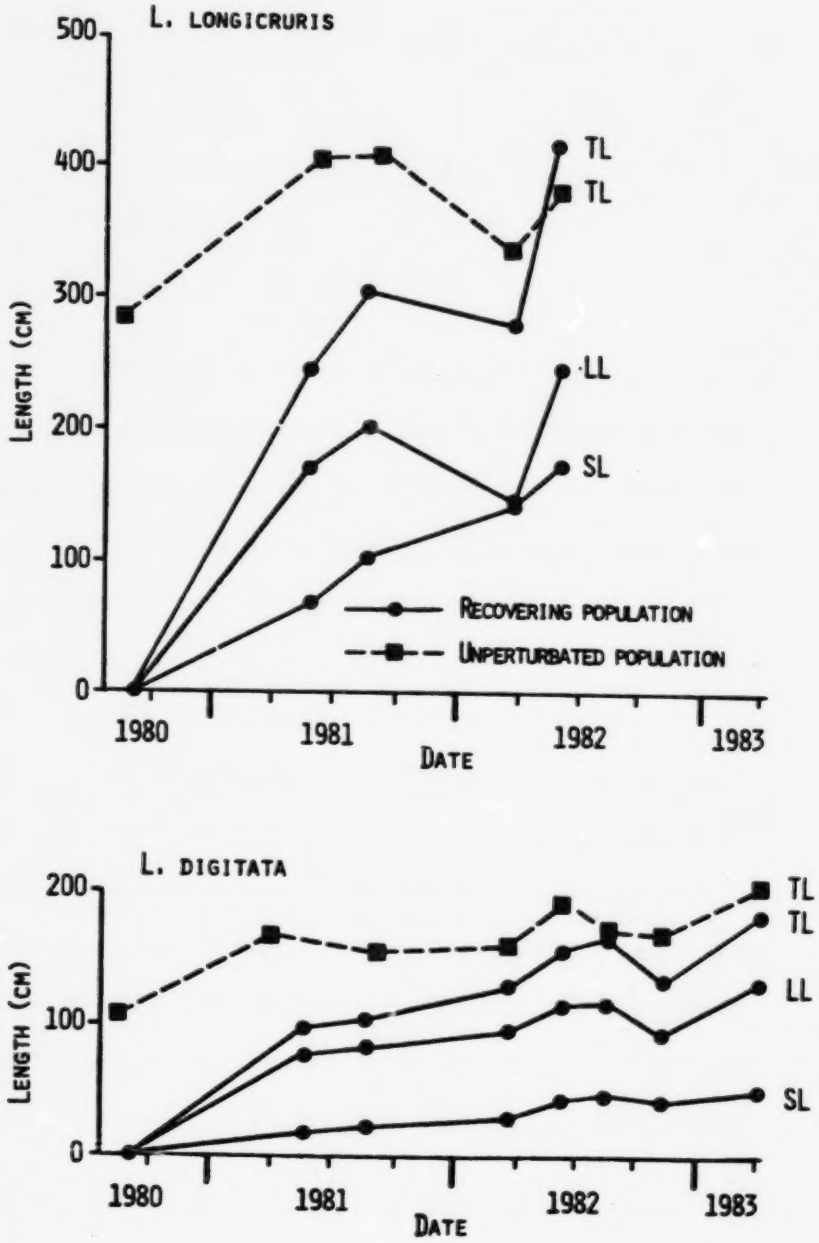
[a] Harvested September 1980

[b] Calculated assuming a linear mortality rate as interpreted from Figure 6.

lived of the two species within this depth range, with some plants living nearly three years after being tagged. Based on their total length and Figure 7, some of the plants which survived longest were probably at least one year old (7 plants >100 cm total length) when tagged, suggesting an estimated maximum life expectancy for L. digitata of at least four years. No L. longicruris plants survived longer than two years and because those surviving longest were small when tagged (<140 cm total length), the maximum life expectancy for L. longicruris is probably about two years. This interpretation is consistent with the evidence of two modes in the L. longicruris histograms in Figure 4. If these modes represent two year classes, a maximum life expectancy of two years is implied.

The growth curves presented in Figure 7 show that two years are required for individual plants of both species to attain a size equal to those of the pre-harvest population. This substantiates data in Table 3 which indicates two years are required for a full recovery from harvesting. Figure 7 also shows that the biomass of plants more than one year old is lowest during winter months due to reduced lamina area. Analysis of the movement of holes punched just above the meristem of the tagged plants revealed seasonal differences in lamina growth and attrition for both species for the period March 1982 until April 1983. Grown and lost lamina biomass was calculated based on the

Figure 7: Mean stipe length (SL), lamina length (LL) and total length (TL) of unperturbated and recovering (0-1 year old, harvested September 1980) populations of L. longicruris and L. digitata within site D. (Minimum n=13)



relationship between lamina area and lamina biomass determined from measurements on collected Laminaria:

L. longicruris: $LB = 0.0730 \times LL \times LW$ ($N=2439$, $r^2=95\%$)

L. digitata: $LB = 0.0699 \times LL \times LW$ ($n=1114$, $r^2=92\%$)

where: LB = lamina biomass (g)
LL = lamina length (cm)
LW = lamina width (cm)

Figure 8 indicates that maximum lamina growth and increase in plant biomass occurred during spring followed by the period of greatest attrition and net biomass loss during the summer months. During autumn and winter, the plants are relatively stable, but there is evidence of gradually increasing plant biomass.

Standing crop biomass of the recovering populations of both species for three years following harvesting is presented in Figure 9. The curves are based on the survivorship of both species within the tagged plant quadrats in the harvest plot. Plant biomass was calculated based on the relationship between lamina area and plant biomass determined from measurements on the previously mentioned collected Laminaria.

L. longicruris: $PB = 0.0919 \times LL \times LW$ ($n=2439$, $r^2=94\%$)

L. digitata: $PB = 0.0872 \times LL \times LW$ ($n=1114$, $r^2=92\%$)

where: PB = plant biomass (g)
LL = lamina length (cm)
LW = maximum lamina width (cm)

Figure 8: Seasonal growth and attrition of L. longicruris and L. digitata lamina within site D for the period March 1982 until April 1983. (Minimum n=11)

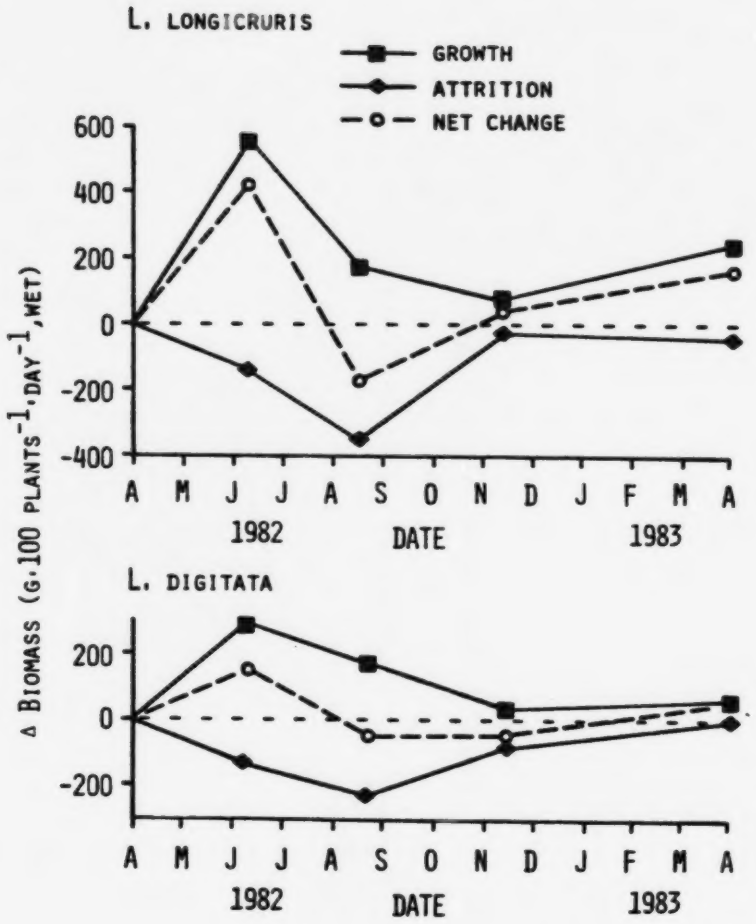
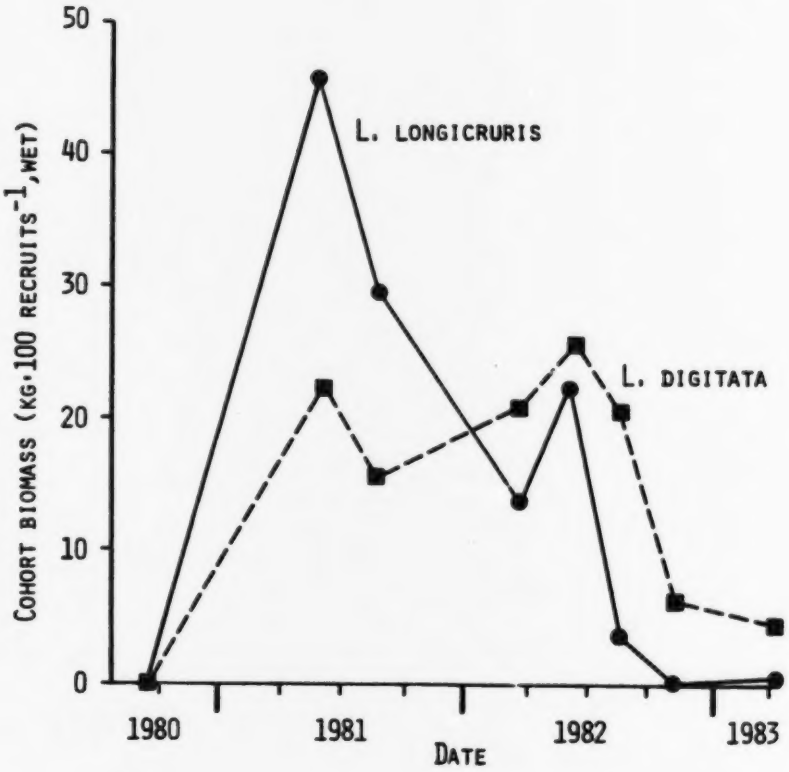


Figure 9: Cohort biomass of 0-1 year old L. longicruris and L. digitata recovering from a September 1980 harvest within site D and first monitored in May 1981.



The maximum yield per recruit for both species occurred the summer following harvesting although for *L. digitata* maximum population biomass occurred two years after harvesting. Three years following harvesting only a small percentage of the biomass attained during the first two years after harvesting remained.

## DISCUSSION

The importance of large kelps in influencing seaweed community development and characteristics has been noted by Paine and Vadas (1969), Kain (1975) and Foreman (1977). Their studies addressed secondary succession on substrate cleared by divers or intensive sea urchin grazing, but conceivably, harvesting of a Laminaria canopy could alter the diversity and stability of the understory community and resilience of the Laminaria population. These are the prime considerations for the development of harvest management strategies which emphasize conservation and long-term optimal utilization of the Laminaria resource, notwithstanding negative indirect effects on higher trophic levels (Wharton and Mann 1981).

Within the shallow site (S) there was a clear distinction of the harvested plot in 1981, one year following harvesting, from the control plot. This distinction was characterized particularly by growth of the epiphytes C. purpureum and C. rubrum, and also the annual thallus of P. palmata. This distinction, however, cannot be attributed to removal of the kelp canopy only in the harvested plot. Kelp biomass was well below preharvest levels in both the control and harvest plots in 1981. The winter of 1980-81 was severe with extensive ice formation in

Lobster Bay. The most likely cause of the decreased Laminaria biomass at site S, considering its shallow depth and exposure to water movement, is ice scouring during January and February 1981. Since both the control and harvested plots were probably subjected to canopy removal by ice, the distinction of the harvested plot in 1981 cannot be unequivocally attributed to the harvest. This argument is reinforced by considering that the three above-mentioned understory species which contributed the most to the distinction of the harvest plot probably grew during the spring of 1981 by which time there would be no substantial difference in the kelp canopy between the control and harvest plots.

For site D a similar argument applies for C. purpureum and C. officianalis which displayed increased biomass and Cladophora sp. and M. alata which displayed decreased biomass within the harvest plot in the summer of 1981. Laminaria canopy recovery was well in progress by December 1980, four months following harvesting, and had substantially recovered by summer 1981. There was no appreciable difference in canopy cover between the control and harvest plots when these four species, interpreted as important contributors to the 1981 harvest plot distinction, were undergoing spring growth. No biological explanation is offered for the observed

differences in understory biomass distribution but, alternatively, it is possible that the sampling pattern did not adequately account for within-plot heterogeneity which may be responsible for the significant differences between control and harvest plot biomass distributions.

Overall, the removal of the Laminaria canopy is judged to have only a minor and reversible effect on the understory community within both sites. Within site S C. purpureum, C. rubrum and P. palmata are annuals attaining maximum biomass during late spring and summer. There is no indication they modify understory composition of the more persistent pernnial species. The dominant perennial species within the site, C. crispus, P. brodiaei, P. membranilolia and F. vesiculosus L. maintained relatively stable biomass distributions based on the interpretation of Table 1. Similarly, for site D C. purpureum, Cladophora sp. and M. alata are annual species which undergo their most rapid growth during spring, and the perennial understory community of C. crispus, P. brodiaei and P. membranifolia remained stable. One possible exception is C. officianalis which decreased in biomass in both the control and harvest plots but less so in the harvest plot. With the rapid recovery of the Laminaria canopy within site D, and the probable potential for its rapid recovery at site S in the absence of ice scouring, no effect on the understory community persisting longer than one year following a single incident of canopy removal is anticipated.

All the evidence in Tables 3 and 4 and Figures 4, 5 and 7 support, or are consistent with, the interpretation that both *L. longicruris* and *L. digitata* recover substantially from harvesting within one year although two years are required for both species to reacquire preharvest population characteristics. The mortality rates of both species together with their rapid regrowth from harvesting indicate high plant turnover, and Figure 9, which incorporates this information, clearly shows that harvesting should occur on a yearly basis to maximize yield for both species. According to Figure 8 harvesting should occur during late spring or early summer to maximize harvest yield since this period follows the rapid growth of the spring and precedes the attrition which occurs during the summer months.

These considerations do not incorporate the possibility of recruitment overharvesting. This is an important consideration since a yearly harvest could severely reduce the reproductive potential of harvested area. If harvesting were to occur on a yearly basis in spring or early summer the recovering population will have had little opportunity to put much effort into reproduction. Chapman (1981) considered the reproductive potential of *L. longicruris* and *L. digitata* and concluded that if stands of reproductive plants were within 600 m (his maximum experimental distance) of an area barren of kelp substantial recruitment was observed, thus these two species are capable of long distance spore dispersal. Yearly harvesting of kelp within a particular area is thus

acceptable from this point of view if only those plants which are easily accessable are harvested, and nearby, less accessable plants are left to provide recruitment.

With recruitment assured, and in light of the data presented here, the conventional wisdom that *Laminaria* plants should be harvested by detaching the lamina above the meristem, thereby facilitating lamina regeneration, may be overly conservative. Indeed, there may be no yield advantage by employing such a harvest strategy. Most plants large enough to be harvested in this manner would probably be about one year old with a remaining life expectancy of less than one year. Another year would be required for those plants to attain a harvestable lamina length by which time very few plants would remain. This argument would be countered by evidence that harvesting above the meristem prolongs life expectancy, but there is presently no reason to suspect this.

The relative abundance and biomass of *L. longicruris* and *L. digitata* within the recovering population at site D in 1981 (Table 4) favored *L. longicruris* by a ratio of 13:1 (abundance) and 4.7:1 (biomass). A shift toward a more even ratio as both the harvest and control plots matured was also noted. This pattern is consistent with there being a competitive interaction between *L. longicruris* and *L. digitata* since the relative success (interpreted as summer biomass) of *L. longicruris* appears to be inversely related to *L. digitata*

biomass. Initially observed is the rapid growth and population recovery of L. longicruris. L. digitata recovers more slowly but because of its higher life expectancy (>4 years) compared to L. longicruris (2 years) it persists and gradually reduces space and/or light opportunities for recruiting L. longicruris. If this scenario is accurate then the development of a mature L. digitata population is undersirable because of its slow growth and its inhibition of faster growing L. longicruris. This evidence further suggests the desirability of a yearly harvest to attain maximum yield.

In conclusion, this study indicates that a yearly harvest of Laminaria within the environs of Lobster Bay, southwest Nova Scotia would maximize yield. The harvest would yield the largest crop during late spring to early summer (May-July). The data acquired in this study do not support the conventional wisdom that plants must be cut above the meristem for conservation reasons, rather whole plants may be removed. The removal must be done by cutting, not pulling, because of the potential damage to the rocky substrate resulting in understory community disruption and the killing of recruiting Laminaria. Two points for caution, however, must be addressed. The effects of successive yearly harvests within a particular area on the understory community has not been determined, and many questions remain regarding the effect of Laminaria removal on fauna associated with the kelp beds (Breen and Mann 1976, Pringle and Sharp 1980).

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